

**GEOGRAPHIC DISTRIBUTION OF THE ANT GENUS *Formica***  
(HYMENOPTERA: FORMICIDAE)

ROBERT E. GREGG, *Department of Biology, University of Colorado,  
Boulder, Colorado 80302*

**ABSTRACT**—The ant genus *Formica* is characterized briefly with respect to the morphology of the worker, female, and male castes. A resumé of the subgeneric divisions of the genus, together with certain diagnostic traits of each subgenus are included. The geographic distribution of *Formica* is treated in greater detail, with the occurrence of various species having direct bearing upon the limits of the range of the genus receiving special attention. A generalized distribution map is provided which attempts only to show the over-all pattern, necessarily omitting minute details of occurrence. The genus is shown to be holarctic, but apparently absent from most of the areas of arctic tundra. The southern boundary in North America embraces the table land of Mexico, the northern portion of Lower California, and all but the southern part of Florida. In the Old World the southern boundary includes northwestern Mediterranean Africa, the Near East to the mountains of Afghanistan, high elevations in the Himalayas, and across central China to the island of Formosa. An isolated occurrence in the Ahaggar Mountains of Africa is recorded. A species claimed to have been found within the tropics (northern Sumatra) is also discussed. And a limited consideration of the difficult topic of altitudinal distribution is attempted.

In Wheeler's (1913) revision of the genus *Formica* L., there were recognized 144 forms representing species, subspecies, and varieties, and these ants were shown to have a broad circumpolar distribution ranging through Europe, most of Asia, and the greater part of North America. Emery (1925) lists 62 full species in the world fauna, with many subspecies and varieties. Since then some forms have been relegated to synonymy, others have been raised from infraspecific to specific status, and in addition new forms have been discovered and described by various authors. It is not the intention, however, of this paper to review or revise the taxonomy of this genus. The group contains the greatest number of ant species in the boreal parts of the world, and is in many respects a dominant assemblage of insects. Very significant advances in our knowledge of *Formica* were made by Creighton (1940) in his re-evaluation of certain members of the *rufa* group, and again (1950) when all North American forms in the genus were thoroughly examined. In the latter work also, the varietal category for all species of ants in our fauna was dropped completely, only the species and subspecies categories being held to be valid. This action greatly improved and simplified both the taxonomy and the nomenclature of ants, and paved the way for other studies in myrmecology. Creighton recognized and treated 95 forms of *Formica* as constituting the New World segment of the genus, and not only

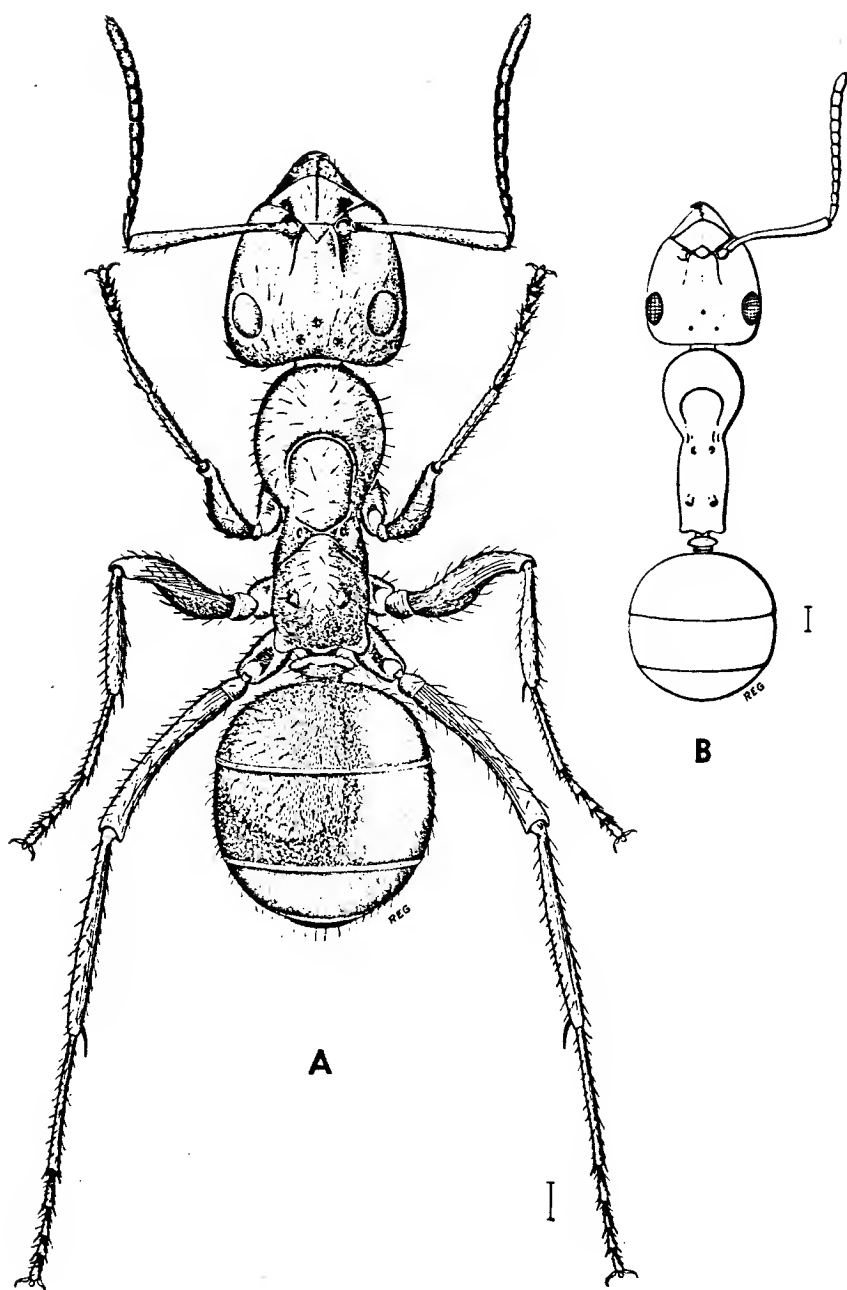


Fig. 1. *Formica obscuripes* Forel. A, large worker; B, small worker.

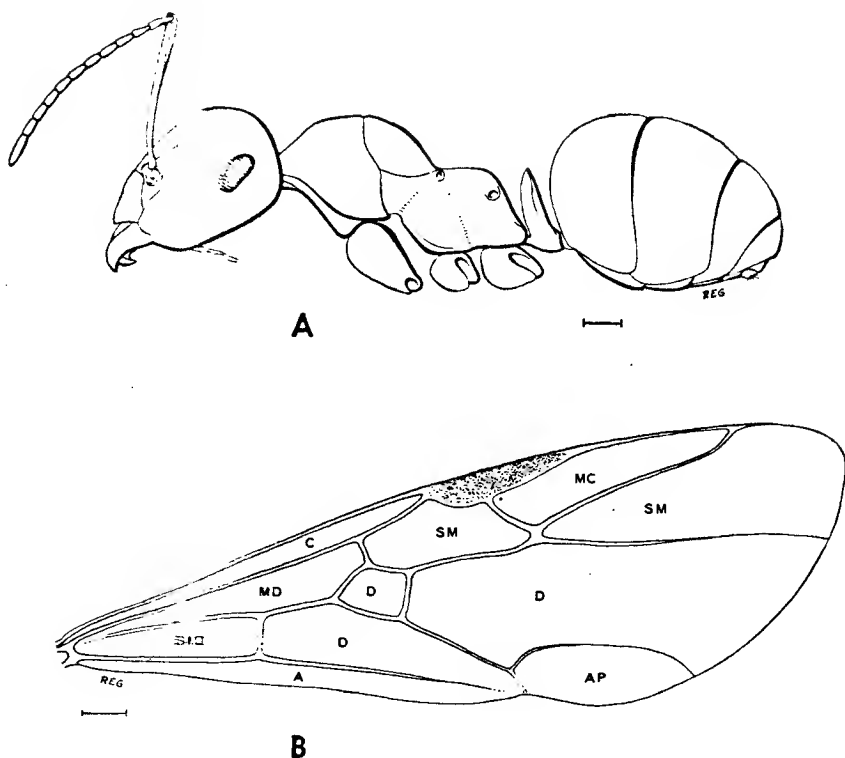


Fig. 2. A, *Formica obscuripes* Forel, lateral view of large worker; B, anterior wing of *Formica mageroides coloradensis* Wheeler. C—costal cell, MC—marginal cell, SM—submarginal cells, MD—median cell, SMD—submedian cell, D—discoidal cells, A—anal cell, AP—apical cell. (Wing terminology follows Borror and DeLong, An Introduction to the Study of Insects, 1964, p. 522.)

was the classification of these ants extensively revised, but a statement concerning the geographic distribution of each taxon was supplied. Wheeler had done this for all the species some 37 years earlier, so far as his data would permit, but Creighton was able to extend the known ranges of many species and to make corrections resulting from the improved taxonomy. From an intensive study of the ants in the State of Colorado alone, I have added many localities for different species of *Formica* and have shown that certain of them tolerate greater altitudinal ranges than previously suspected (Gregg, 1963). The Catalog of Hymenoptera for America North of Mexico (sections on Formicidae by M. R. Smith, 1951, 1958, 1967) gives the distributions of species in a very general way by citing the states and provinces from which each has been recorded. Various persons are actively engaged in the collecting of ants, and it is to be expected that

many gaps in the known ranges of all the species will continue to be filled.

The present contribution is an attempt to summarize the salient taxonomic features of the genus *Formica*, based primarily on the worker caste, and to provide a generalized distribution map for the group as a whole. The nomenclature and diagnoses that follow conform to those of Emery (1925).<sup>1</sup>

### Genus *Formica* Linné

*Formica* (part.) Linné, *Systema Naturae*, 10th ed., 1758, p. 579; Emery, *Genera Insectorum*, 1925, Fasc. 183, p. 241.

#### Characteristics:

**Worker.**—Size and shape of species variable; usually monomorphic though some forms, particularly in the *rufa* group, are more or less polymorphic. Eyes placed toward the posterior portion of the head, well developed and consisting of many facets; ocelli distinct. Mandibles broad with a denticulate apical border. Maxillary palps 6-segmented, except in a few forms of *F. exsecta* Nylander, with the 4th article a little longer than the 5th; labial palps 4-segmented. Funicular segments of the antenna diminishing in length from the second to the penultimate, except in the subgenus *Proformica* Ruzsky. Dorsum of the thorax more or less deeply impressed in front of the epinotum; metanotum reduced to a narrow band across the thoracic dorsum; metathoracic spiracles dorso-lateral but well separated. Scale of the petiole vertical or slightly inclined, the superior border either sharp or rounded, in some cases blunt and truncated. The crest may also be entire or notched (fig. 1, A and B; fig. 2, A).

**Female.**—Ordinarily much larger than the worker of the same species, however, in some species the queens are no larger than the major worker and may even be smaller (*microgyna* group and some members of the *rufa* group). Mesonotum moderately elevated above the pronotum but not overhanging it. Anterior wing with two closed discoidal cells and one open discoidal (fig. 2, B).

**Male.**—About the same size as the female in most species; in those species with diminutive females, the males may be larger. Masticatory border of the mandible rarely toothed, but mandible never linear. Genitalia robust, stipes lacks appendage. Anterior wing furnished with discoidal cell, except in *F. krausi* Forel.

### SUBDIVISIONS OF THE GENUS *Formica* (workers and females)

#### Subgenus *Proformica* Ruzsky

Funicular segments two and three together only slightly longer than the first, and often no longer than the first.

<sup>1</sup> In the recent paper by Buren (1968) on certain aspects of the taxonomy of *Formica*, I am in accord with some of his conclusions. However, I do not agree for example, with his proposal to raise *Proformica* to generic rank, nor with the suggestion that subgenus *Ncoformica* should be abandoned. The subgenus *Proformica* could be restricted to those Old World species which conform closely to the characters of *Formica nasuta*, especially to its mandibular dentition, as given by Buren. As stated above, this article concerns primarily the general geographic distribution of *Formica*, not a revision of its nomenclature.

### Subgenus *Formica* Linné

Antennal scape no longer or only slightly longer than the distance from the center of the clypeal border to the center of the occipital border. Epinotum usually angular. Contains *fusca*, *rufa*, *microgyna*, and *exsecta* groups.

### Subgenus *Raptiformica* Forel

Anterior clypeal border with a median concave emargination which may be narrow and pronounced or shallow and inconspicuous.

### Subgenus *Neoformica* Wheeler

Antennal scape always notably longer than the distance from the center of the clypeal border to the center of the occipital border. Head relatively long and narrow. Epinotum with rounded dorsal profile, basal and declivious faces not sharply separated.

## DISTRIBUTION

The zoogeography of *Formica*, as will be seen from the accompanying map (fig. 3), is extremely broad in the northern hemisphere. This map, it must be remembered, represents a number of compromises and therefore has to be generalized. It is quite impossible on a world chart of so small a scale to show all the minutiae of distribution; furthermore, not all the desirable details are available and won't be until all regions are intensively searched for specimens. Although our collection contains a very large number of records from North America, and a substantial number also from Europe and from Asia, no attempt is made to place locality dots on this map because sufficient accuracy could not be achieved and their presence would probably clutter the picture. A large scale map with dots large enough to register when reduced to page size would certainly render the dots fused into a shaded map. Therefore, in attempting to delineate here the circumpolar distribution of a genus, I am obliged to employ one type of shaded map. The actual boundaries portrayed are smoothed owing to the impracticality of trying to show the precise limits toward the edges of a range. There are, no doubt, isolated outliers of the group that exist in ecologically suitable sites beyond the territory that is generally favorable to these ants. Thus large areas in Mexico, in North Africa, and in Persia are included within the boundaries, whereas in fact few colonies are adapted to exist in such places. The occurrence of the ants there must be very discontinuous, for in these arid regions only local spots with enough permanent moisture would be expected to support the insects. In Mexico, for example, *Formica* is able to live in the higher mountains, but its distributional pattern is "spotty." Both the Sierra Madre Oriental and the Sierra Madre Occidental represent high-level pathways from southwestern United States into tropical Mexico. There are gaps in both pathways, but the elevations in each mountain range are high enough to support Nearctic fauna and flora along the crests. West of Durango, at altitudes of 8000 feet or more,

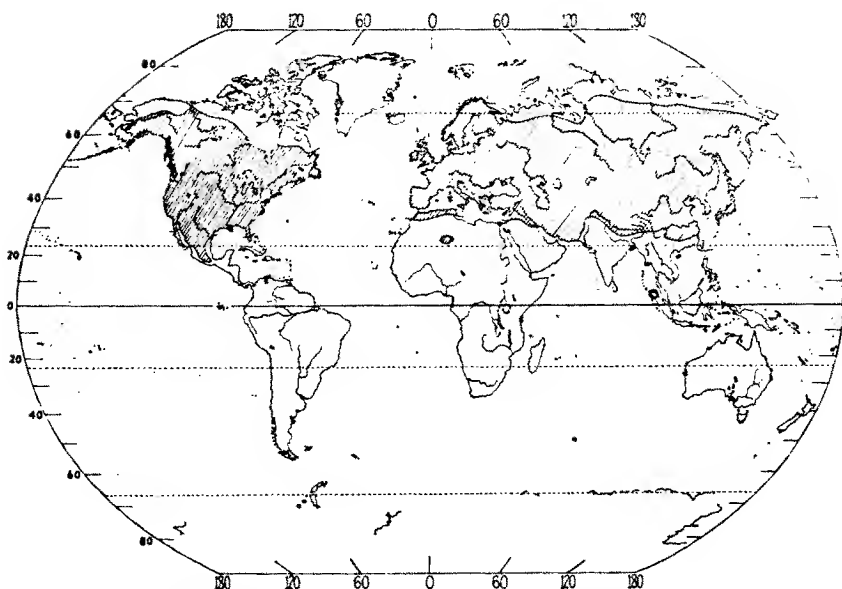


Fig. 3. Geographic distribution of the genus *Formica* Linné.

there are pine groves essentially similar to those in the mountains of southern Arizona, and the same is true of the eastern Sierra, although only broken ranges in Coahuila serve to connect it with the Chisos Mountains of Texas (Creighton, in litt.). Similar discontinuities must attend the distribution of *Formica* at extremely high arctic and sub-arctic latitudes, but the factors involved (e.g. low temperature) are obviously different, or their combined effects operate in a different manner. Mountain ranges of high elevation are also blanketed by the symbol for the occurrence of *Formica*, despite the fact that the known distribution for these ants does not include the very high altitudes above timberline and above snowline on most ranges. It would be futile to indicate the upper altitudinal boundaries on this kind of map, though I have elsewhere tried to show these limits for certain species in the Rocky Mountains of Colorado, where a few forms do establish colonies in the alpine zone. Based on experience in these mountains, I have also pointed out the unreliability of certain altitudinal records cited by previous authors (Gregg, 1963). This map, then, is an estimate of the probable overall territory in which the genus *Formica* occurs.

The greatest number of species of *Formica* in North America appear to be dispersed between the parallels of 35° and 50° north latitude, and in Eurasia between 40° and 55°. Actually, this is an over-simplification since the area of greatest concentration of species may depart

radically from these parallels in particular regions, as, for instance, in eastern North America where a rich assortment of forms by no means reaches as far north as 50°. Although the total horizontal range of the genus in North America extends from beyond the Arctic Circle to the Tropic of Cancer and below, there is a notable disappearance of species as one proceeds toward these extremes. A few forms are decidedly boreal (or while widely dispersed may tolerate far northern conditions) and may be found from central Alaska and interior Canada to Labrador and Newfoundland. Examples of these include such ants as *F. fusca* L., *F. sanguinea subnuda* Emery, *F. marcida* Wheeler, and the subspecies of *F. neorufibarbis* Emery. In a similar manner, the hot and arid Sonoran areas of southwestern North America support a very meager sample of species, and the ones usually found are *F. perpilosa* Wheeler, *F. pilicornis* Emery, and *F. rufibarbis gnava* Buckley in appropriate parts of their respective ranges. Other species may reach quite far south in Mexico, but characteristically they occur at elevated stations in mountainous terrain.

It will be useful to point out those records which seem to represent the most remote localities for any species of the genus. In 1913 Wheeler reported on *Formica* collected by W. M. Mann at several localities in the State of Hidalgo, Mexico, primarily at Guerrero Mill, elevation 9000 feet. The species involved were *F. microgyna rasilis* var. *nahua* Wheeler, *F. subcyanea* Wheeler, *F. rufibarbis gnava*, and *F. cinerea altipetens* Wheeler. Wheeler gives other Mexican localities also and the species found therein as follows: *F. perpilosa* in Coahuila, *F. fusca* (probably *argentea* Wheeler) from Durango at 8100 feet and from Atoyac in Vera Cruz, *F. rufibarbis* (probably *occidua* Wheeler) from Sonora and Omilteme in Guerrero, *F. rufibarbis* (probably *gnava*) from Durango at 8100 feet, and *F. rufa obscuripes* Forel, whose exact location in Mexico is unknown, but which he thinks may occur in the mountains of northern Mexico. The precise identification of the last form seems also to be in doubt. All of these records, with the exception of *perpilosa*, were attributed to Forel.

In 1922, Wheeler discussed the presence of *Formica* in far southern and in tropical locations. Most of these records are considered not to be representative of the original range of *Formica*. *F. rufibarbis* F. cited from Pretoria, South Africa, by Bingham is the only instance from the southern hemisphere, but Wheeler regards this case as a direct importation from Europe. He also agrees with Emery that *F. fusca glebaria* Nylander, a common species in southern Europe, has been introduced into the gardens of Algiers through human activity. Among ants received from Dumaguete, Island of Negros, Philippines, Wheeler recognized two species, *F. fusca* and *F. neogagates lasioides* Emery, which appeared to be identical with North American

specimens of these ants, and he concluded that they must have been inadvertently imported from the United States in materials for several Americans who were teaching at the Silliman Institute in Dumaguete. In a later paper (1927), however, he decided that these specimens had probably been left in some vials which Dr. Chapman took with him when the latter left Boston for the Philippines!

Despite the fact that the foregoing records have been disposed of as unnatural, Wheeler believes that two cases exist of tropical relicts in the genus *Formica*. Again in 1922, he regards *F. picea* var. *formosae* Forel, which had been collected at Taihorin, Formosa, as probably part of the indigenous fauna of that island. The typical *picea* is a boreal ant of the peat bogs of Europe, so Wheeler infers that since the mountains of Formosa rise to great heights (9000 to 14,000 ft.), Forel's variety may be resident at considerable elevations as remnant populations under climatic conditions not unlike those in northern Europe. I have therefore included Formosa in the range map of the genus, but until further collections can be made to substantiate these assumptions, this extension of occurrence may be accepted with some doubt. Emery (1925) records another species, *F. obsidiana* Emery also from Formosa. That any form of *Formica* should occur so far into the tropics as northern Sumatra, within 5° of the Equator, seems incredible. However, Wheeler (1927) described a new variety, *F. fusca* var. *fairchildi*, from Kota Dah, Sumatra, taken in a pine forest at an altitude of 4000 feet. The specimens are obviously close to the typical *fusca*, but according to the description are nevertheless distinct. Wheeler's reasons for believing this ant to be a true tropical relict include the remote locality of its occurrence, the considerable altitude of the station, and its pine forest habitat. He further points out that *F. fusca* is closely allied, if not identical, with *F. flori* Mayr found in the Baltic Amber, of Oligocene age, which preserves numerous examples of tropical, subtropical, and warm temperate organisms. Thus *Formica* could at one time have had a much wider distribution, and its present restriction mostly to boreal temperate regions could be a more recent phenomenon. Wheeler postulates that more investigations in the higher altitudes of Sumatra, and even of Borneo and Java, may show isolated surviving populations of some form of *fusca*. The above suppositions are at least plausible, and may be accepted tentatively until further information comes to hand. I have included Sumatra on the map, but have used only an open circle to indicate justifiable uncertainty. If *Formica* is ever unquestionably demonstrated from Indonesia, or other comparable tropical regions, it is logical to expect the species to represent some variant of *fusca* since this ant is the most eurythermic and most adaptable member of the genus.

Other southern extremities of distribution for the genus *Formica*



have been extracted from the summary presented by Emery (1925) in the Genera Insectorum. *F. rufibarbis* var. *clarissima* Ruzsky (Emery) is cited from Zaidam (or Cham-e Zeydun, Iran) near the coast at the head of the Persian Gulf. *F. subcyanea* is listed for the state of Guerrero, Mexico (and according to Wheeler at about lat. 18°). In North Africa, *F. (P.) menozzii* Santsehi occurs at Ain Sefra, Algeria, and *F. (P.) kraussi* Forel is known only from southern Algeria, and since most of this region is intense desert, I presume the area to be the Ahaggar Mountains or surrounding plateau. This species must be a relict from a moister geological period in the Sahara when the continuous range of *Formica* may have included much more of northern Africa than it does today. *F. fusca* var. *pyrenaea* Bondroit has been recorded from Morocco.

The species, *Formica emmae* Forel, comes from Biskra, in northern Algeria, and is in certain ways a very unusual ant. It resembles *Cataglyphis* Förster in that the fourth maxillary joint is curved and unusually long, the thorax saddle-shaped, the petiole is thick, and the mentum bears ammochaetae. Wheeler treated it in 1913 as a species of *Proformica* (as Forel had done in 1909). Forel made it the representative of a separate subgenus, *Paraformica* Forel, in 1915, and Wheeler followed this lead in 1922. Then in 1925, Emery elevated *Paraformica* to full generic rank, which is probably the correct procedure, but in view of the nomenclatural history of this ant, I think we may rightfully include the insect in the present discussion.

*Formica pilicornis* is characteristic of the foothills of the Coastal Range of central and southern California, and according to Creighton (1950) it reaches into Lower California. However, the existence of *Formica* in Baja California is very likely restricted to the northern end of the peninsula. There, only the Sierra Juarez and the Sierra San Pedro Martir support stands of pine at their crests, and hence offer a highway for Nearctic species. In the central portion of the peninsula, the mountains are bare except for xerophytic shrubs, and in the southern part the vegetation is composed of thorn forest. Neither of the latter two situations is conducive to the occurrence of boreal ants.

Documentation of the most northern records of occurrence of *Formica* can be obtained in part from several papers of Wheeler (1913, 1917, and 1922), and may be summarized in the following manner. In Europe it has been found at North Cape which is beyond 70° N. In Asia (1913, footnote, p. 384) it is reported, and presumably represented by *F. fusca*, as far north as 67° 34' at Verchojansk (Verkhoyansk) on the Jana River in Siberia. *F. picca* Nylander is a cold stenotherm that is broadly distributed across all of northern Europe and Asia to China and eastern Siberia. In North America, *F. fusca* and *F. marcidula* were reported from Fort Yukon on the Arctic Circle,

and *F. neorufibarbis gelida* Wheeler has been taken at Rampart and Nulato, Alaska, both of which are approximately 65° N. Other Alaskan localities for various species of *Formica* include Metlakatla, Ketchikan, Sitka, Skagway, Homer, Seward, Kasiloff Lake on the Kenai Peninsula, and Kodiak Island. Whitehorse, Yukon Territory, Canada, has also yielded several of the above species. Eastward, *F. fusca* is found as far north as Point Comfort on James Bay, Quebec, in New Brunswick, Nova Scotia, and Newfoundland. Wheeler also reports *F. fusca gelida* (the form now regarded as the subspecies *algida* Wheeler of *F. neorufibarbis*) from such northeastern stations as Anticosti Island, Quebec, several localities in Newfoundland, and Square Island and St. Lewis Inlet, Labrador. By far the northernmost site for the genus in the New World is that of the Mackenzie River Delta, reported by Brown (1949), where nests of *F. fusca* were found by Marie Hammer. This occurrence is well above the Arctic Circle.

The altitudinal range of *Formica* is impressive, being known from sea level in most parts of its distributional territory to relatively high elevations in numerous mountain systems. Wheeler notes *fusca* from as much as 2400 meters (7872 ft.) in the Alps. I have collected *Formica pratensis* Retzius at 6275 feet near Montanvers, above Chamonix, France. In North America, Wheeler (1913) gives altitudinal data for a few species that were known at that time to reach remarkably high elevations, and some of his figures follow: *F. fusca* 10,200 ft.; *sanguinea subnuda* 12,000 ft.; *dakotensis montigena* Wheeler 11,500 ft.; *adamsi alpina* Wheeler (now *whymperi alpina*) 11,000 ft.; *fusca argentea* 11,000 ft.; *fusca subaenescens* Emery (= *fusca*) 11,000 ft.; and *fusca gelida* (now *neorufibarbis gelida*) 13,000 ft. *F. subaenescens* was also reported from 7000 feet in British Columbia, and *F. gelida* from 3840 feet on Mt. Washington, New Hampshire, which represent environmental conditions that are to be found at approximately two to three times these elevations, respectively, in the Rocky Mountains of Colorado and New Mexico.

I have recently published data (Gregg, 1963, 1964) extending the altitudinal limits of *Formica* in Colorado, and these possibly represent the maxima for the continent. There follow the most striking examples for high altitude residency (established colonies): *F. altipetens* 11,000 ft.; *cinerea lepida* Wheeler 11,000 ft.; *rasilis densiventris* Viereck 11,542 ft.; *whymperi alpina* 12,500 ft.; *integroides coloradensis* Wheeler 11,600 ft.; *dakotensis montigena* 11,500 ft.; *fusca* 12,500 ft.; *fusca argentea* 11,000 ft.; *sanguinea subnuda* 13,000 ft.; *neorufibarbis* 11,542 ft.; and *neorufibarbis gelida* 14,260 ft. While this final record is based upon a worker specimen taken at the summit of Mt. Evans by Dr. Harold Grant, we have been unable to duplicate the find or to discover actual colonies. The species is, however, quite common at high alti-

tude, reaching its greatest abundance between 10,500 and 12,000 feet. Unequivocal records of *gelida* have been obtained as high as 13,500 feet.

In Mani's study (1962) of the insects of the North-West Himalayas, there are brief references to the ants of this region. He regards all territory above timberline (approx. 3000 m. or 9840 ft.) as the nival zone, (I would restrict the term "nival" to the zone of perpetual snow, that is, above snowline) and states that more than a dozen species of ants occur widely in this zone. These include *F. gagates* Latreille, *F. truncicola* Nylander, and *F. picea*, which are also broadly distributed in north and central Europe, Tibet, and in north and central Asia. *F. picea*, he reports, extends from 2800 meters (9186 ft.) to 4800 meters (15,744 ft.), making this the highest known occurrence for the genus *Formica*. It is still considerably below the line of permanent snow, which is placed by Mani in excess of 5000 meters (or more than 16,400 ft.) in the western Himalayan ranges.

In summary, the distribution of *Formica* is essentially holarctic, except for most of the extreme northern portions of the Eurasiatic and North American continents, the Arctic islands, Greenland, and Iceland. It is absent also from southern Florida, probably from most of Mexico, and from islands off the west coast of Africa. It has been introduced, according to Emery, into Corsica and Sardinia. Ectopic locations include the Ahaggar Mountains, and possibly high elevations in northern Sumatra.

#### ACKNOWLEDGMENTS

The author gratefully acknowledges support for this work by the National Science Foundation, Grant GB 2165, and academic leave for 1965-66 by the University of Colorado. My wife, Ella Virginia Gregg, has assisted in all aspects of field work. Dr. W. S. Creighton has reviewed the manuscript and contributed helpful improvements.

#### REFERENCES

- Brown, W. L. 1949. A few ants from the Mackenzie River Delta. Ent. News 60:99.
- Buren, W. F. 1968. Some fundamental taxonomic problems in *Formica*. Jour. Georgia Ent. Soc. 3:25-40.
- Creighton, W. S. 1940. A revision of the North American variants of the ant *Formica rufa*. Amer. Mus. Novit. No. 1055, 10 pp.
- . 1950. The ants of North America. Bull. Mus. Comp. Zool. 104: 1-585.
- Emery, C. 1925. Hymenoptera: Family Formicidae; Subfamily Formicinae. Gen. Insect., Fasc. 183, pp. 241-261.
- Gregg, R. E. 1963. The ants of Colorado. Univ. Colo. Press, Boulder, 792 pp.
- . 1964. Distribution of the ant genus *Formica* in the mountains of Colorado. In Natural History of the Boulder Area, Univ. Colo. Mus., Leaflet No. 13, pp. 59-69.

- Mani, M. S.** 1962. Introduction to high altitude entomology. Insect life above the timber-line in the North-West Himalya. Methuen & Co. Ltd., London, 302 pp.
- Smith, M. R.** 1951. In Muesebeck *et al.*, Hymenoptera of America north of Mexico, Synoptic Catalog. U. S. Dept. Agr., Agr. Monogr. 2:778-875.
- . 1958. In Krombein *et al.*, Hymenoptera of America north of Mexico, Synoptic Catalog, First Supplement. *ibid.* pp. 108-162.
- . 1967. In Krombein *et al.*, Hymenoptera of America north of Mexico, Synoptic Catalog, Second Supplement. *ibid.* pp. 343-374.
- Wheeler, W. M.** 1913. A revision of the ants of the genus *Formica* (Linné) Mayr. Bull. Mus. Comp. Zool. 53:379-565.
- . 1914. The ants of the Baltic Amber. Schrift. Physik-ökonom. Gesell. Königsberg 55:1-142.
- . 1917. The mountain ants of western North America. Proc. Amer. Acad. Arts Sci. 52:457-569.
- . 1917a. The ants of Alaska. Bull. Mus. Comp. Zool. 61:15-22.
- . 1922. Ants of the genus *Formica* in the tropics. Psyche 29:174-177.
- . 1922a. Contributions to a report on the ants of the Belgian Congo. Bull. Amer. Mus. Nat. Hist. Vol. 45: Pt. 7, Keys to the genera and subgenera of ants, pp. 631-710.
- . 1927. The occurrence of *Formica fusca* L. in Sumatra. Psyche 34:40-41.
- Wilson, E. O. and W. L. Brown.** 1955. Revisionary notes on the *sanguinea* and *neogagates* groups of the ant genus *Formica*. Psyche 62:108-129.